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1 Individual movement features during prism adaptation
2 correlate with after-effects and interlimb transfer

3
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21
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25 **Abstract**

26 The human nervous system displays such plasticity that we can adapt our motor behavior to
27 various changes in environmental or body properties. However, how sensorimotor adaptation
28 generalizes to new situations and new effectors, and which factors influence the underlying
29 mechanisms, remains unclear. Here we tested the general hypothesis that differences across
30 participants can be exploited to uncover what drives interlimb transfer. Twenty healthy adults
31 adapted to prismatic glasses while reaching to visual targets with their dominant arm. Classic
32 adaptation and generalization across movement directions were observed but transfer to the
33 non-dominant arm was not significant and inter-individual differences were substantial.
34 Interlimb transfer resulted for some participants in a directional shift of non-dominant arm
35 movements that was consistent with an encoding of visuomotor adaptation in extrinsic
36 coordinates. For some other participants, transfer was consistent with an intrinsic coordinate
37 system. Simple and multiple regression analyses showed that a few kinematic parameters
38 such as peak acceleration (or peak velocity) and variability of movement direction were
39 correlated with interlimb transfer. Low peak acceleration and low variability were related to
40 extrinsic transfer while high peak acceleration and high variability were related to intrinsic
41 transfer. Motor variability was also positively correlated with the magnitude of the after-effect
42 systematically observed on the dominant arm. Overall, these findings on unconstrained
43 movements support the idea that individual movement features could be linked to the
44 sensorimotor adaptation and its generalization. The study also suggests that distinct
45 movement characteristics may be related to different coordinate frames of action
46 representations in the nervous system.

47 **Introduction**

48 Whenever we learn something, we often would like it to generalize to other conditions: for
49 instance, we may hope that learning tennis will also result in improvements in table tennis and
50 squash. However, the sensorimotor system needs some specificity, so that each action is
51 optimal in its own context. Some skills in tennis, such as prediction of ball bouncing, should
52 thus not be generalized to other contexts such as squash. In the present study, we probed the
53 generalization of sensorimotor adaptation by assessing how adapting to a new visuomanual
54 relationship transfers across effectors.

55 Research on the transfer of short-term adaptation between the arms revealed the
56 existence of two motor representations in the human nervous system: an effector-specific
57 representation and an effector-independent representation (Wang & Sainburg 2003; Morton &
58 Bastian 2004; Vangheluwe et al. 2006; Taylor et al. 2011; Joiner et al. 2013; Mostafa et al.
59 2014). Such effector-independent representation would underlie the interlimb transfer of
60 sensorimotor adaptation, which also appears to be shaped by contextual conditions (Krakauer
61 et al. 2006) and the cause of motor errors (Berniker & Kording 2008). Generalization is also
62 likely influenced by the kinematic properties of movements, as sensorimotor adaptation was
63 found to generalize across movement speeds to a certain limit (Kitazawa et al. 1997). Indeed,
64 Kitazawa et al. (1997) showed that when movements performed during prism adaptation were
65 fast, the after-effect was greater when movements in the generalization phase were also fast
66 compared to when movements were slower. In fact, this study showed that prism adaptation
67 was not entirely specific to movement speed but also that any difference between the training
68 conditions and the test condition could limit generalization, with the greater the difference,
69 the smaller the generalization. It has also been suggested that motor variability is linked to the
70 adaptation process (Wu et al. 2014). Wu et al. (2014) reported that higher task-relevant motor
71 variability during baseline was correlated with faster adaptation. But as a recent meta-analysis

72 (He et al. 2016) did not confirm this correlation between motor variability and adaptation rate,
73 it is currently hypothesized that motor variability may in part reflect active exploration of
74 movement parameter space in order to optimize sensorimotor adaptation (Pekny et al. 2015;
75 Therrien et al. 2016). Despite the body of work on these issues, the factors and mechanisms
76 modulating generalization of sensorimotor adaptation remain unclear. Here we tested the
77 hypothesis that specific kinematic characteristics of movements may be linked to the
78 interlimb transfer of sensorimotor adaptation.

79 Lefumat et al. (2015) reported substantial individual differences in interlimb transfer
80 of force-field adaptation but also showed that transfer can be qualitatively and quantitatively
81 described for each young individual based on motor variability and velocity during
82 adaptation. Based on these data, Lefumat et al. (2016) could predict the transfer of older,
83 neurological patients suffering from a massive proprioceptive deafferentation. Considering
84 these studies and others (Wu et al. 2014; Therrien et al. 2016), we tested in the present study
85 the hypothesis that movement variability is linked to interlimb transfer based on another
86 classic adaptation paradigm, the prism adaptation paradigm (Harris 1963; Held & Freedman
87 1963; Redding & Wallace 1988; Martin et al. 1996; Kitazawa et al. 1997; O'Shea et al. 2014).
88 The previous findings on interlimb transfer of force-field adaptation may not apply to the
89 interlimb transfer of visuomotor adaptation because distinct neural mechanisms appear to
90 underlie adaptation to new visuomotor mappings (using a visuomotor rotation or prismatic
91 glasses for instance) and adaptation to new limb dynamics (Haith & Vijayakumar 2009;
92 Donchin et al. 2012). Given these differences, we hypothesized that the factors which
93 correlate with the interlimb transfer of prism adaptation would differ from those identified in
94 previous studies on adaptation to a velocity-dependent force field (Lefumat et al. 2015). More
95 specifically, we expected movement variability to influence the interlimb transfer of prism
96 adaptation more than movement velocity.

97 To facilitate the comparison between prismatic and force-field adaptation, we used the
98 protocol and setup of Lefumat et al. (2015) but with a prismatic instead of dynamic
99 perturbation. Although interlimb transfer of prism adaptation has sometimes been found to be
100 non-significant (Kitazawa et al. 1997; Martin et al. 1996; Michel et al. 2007), we
101 hypothesized based on several previous studies (Harris 1963; Cohen 1967; Cohen 1973; Taub
102 & Goldberg 1973; Choe & Welch 1974; Wallace & Redding 1979) that interlimb transfer
103 would be observed in the form of an after-effect on the first movement made after prismatic
104 adaptation, without prisms, with the opposite, non-exposed arm. We reasoned that the
105 presence of an after-effect would indicate the presence of interlimb transfer, but also that the
106 direction of the after-effect would allow us to determine whether visuomotor adaptation is
107 encoded in extrinsic or intrinsic coordinates (Criscimagna-Hemminger et al. 2003; Carroll et
108 al. 2014; Stockinger et al. 2015). Specifically, when using prisms displacing the visual field
109 rightward, encoding of dominant-arm adaptation in extrinsic coordinates (associated with a
110 leftward compensation) would predict a leftward after-effect on the non-dominant arm. In
111 contrast, encoding in intrinsic coordinates (associated with shoulder and elbow abduction for
112 instance) would predict a rightward after-effect. Lastly, because the degree of handedness has
113 been shown to affect motor control and interlimb transfer (Chase & Seidler 2008; Sainburg
114 2014; Lefumat et al. 2015), we tested a mixed set of right- and left-handers in order to provide
115 a general model of interlimb transfer of prism adaptation.
116

117 **Methods**

118 *Participants*

119 Twenty young adults (thirteen men, seven women, mean age: 23.5 ± 2.7 years) participated in
120 the experiment. None of the participants declared a sensorimotor or a neurological deficit.
121 Participants had normal vision or corrected-to-normal vision with contact lenses. Handedness
122 was assessed with the 10-item version of the Edinburgh inventory (Oldfield 1971). Eight
123 participants with a laterality quotient (LQ) between -100% and -10% were classified 'left
124 handed' and twelve participants were classified 'right handed' (LQ between +60% to
125 +100%).

126 Participants gave their written informed consent prior to the study, which was
127 approved by the institutional review board of the Institute of Movement Sciences and was
128 performed in accordance with the standards of the Declaration of Helsinki (1964).
129 Participants were naive to the purpose of the experiment and were informed that they could
130 stop the experiment at any moment.

131

132 *Experimental setup*

133 Seated participants were asked to reach toward flashed visual targets. On a horizontal board,
134 at waist level, a visuo-tactile landmark (a circular hole of 2 cm in diameter) indicated the
135 starting hand position. Visual targets were red light-emitting diodes (3 mm in diameter).
136 Figure 1 shows that three targets were positioned on a 37-cm radius circular array at 0 deg.
137 (straight-ahead), +20 deg. (to the right) and -20 deg. (to the left) with respect to start position.

138 For the entire experiment, participants viewed the set-up and their arm binocularly
139 through specific goggles which allowed vision only through the prism lenses (O'Shea et al.
140 2014). One set of goggles was standard (control) and the other was equipped with Fresnel 3M
141 Press-on plastic lenses (3M Health Care, Specialties Division, St Paul, Minn., USA) as in

142 Martin et al. (1996). The 30-diopter (~17 deg.) lenses were mounted base-left (thus producing
143 a rightward deviation of the visual field).

144 Infrared active markers were taped to the right and left index fingertips, whose
145 positions were sampled at 350 Hz using an optical motion tracking system (Codamotion cx1
146 and MiniHub, Charnwood Dynamics Ltd, Leicestershire, UK). The experimenter controlled
147 the tracking system and the presentation of the visual targets from an adjacent room by using
148 a customized software (Docometre) governing a real-time acquisition system (ADwin-Pro,
149 Jäger, Lorsch, Germany).



150

151 *Figure 1: Experimental conditions, illustrated with a right-handed participant. During the*
152 *PRE-exposure phase, participants reached toward one of three visual targets with the*
153 *dominant and the non-dominant arms. During the exposure phase, participants reached*
154 *toward the central target with the dominant arm while wearing prisms. During the POST-*
155 *exposure phase, participants reached toward one of three targets with the non-dominant arm*
156 *and then with the dominant arm. (Color not required for printed version).*

157

158

159 *Experimental procedure*

160 At the beginning of each trial, participants had to actively position their specified (left or
161 right) hand at the starting location (Figure 1). They were asked to reach as fast and accurately
162 as possible with their index finger toward the visual target, which was illuminated for 0.3 s.
163 Participants were also instructed to 'reach in one movement' and not to correct their position
164 after their finger contacted the horizontal board. No instructions were given with respect to
165 hand path. 1.6 s after trial onset, a 100-ms tone informed the participant to go back slowly to
166 the starting location. 7.4 s after trial onset, a 600-ms tone signalled to the participant that the
167 trial had ended and that the next trial would start immediately. All participants were
168 familiarized with the task during a preliminary phase.

169 To assess the interlimb transfer of sensorimotor adaptation, we employed a procedure
170 inspired by DiZio and Lackner (1995) and Martin et al. (1996) in order to compare non-
171 dominant arm performance just before and just after dominant arm performance with prisms.
172 The experimental session consisted of 3 phases, illustrated on Figure 1:

- 173 – PRE-exposure phase (baseline): Participants executed 30 reaching movements with the
174 dominant arm (DA) then 30 with the non-dominant arm (NDA) toward one of the three
175 possible targets (10 trials per target for each hand). Trials toward the different targets were
176 presented in a pseudorandom order which was similar for all 20 participants. When the
177 PRE-adaptation phase was over, a 2-min break was given, goggles were removed and the
178 control goggles previously worn by participants were discretely replaced with prismatic
179 glasses. During the break, participants had to keep their eyes closed and stay motionless.
- 180 – Prism exposure phase: Participants performed 100 movements with the dominant arm
181 (DA) toward the central target (0 deg.) while wearing the prisms deviating the visual field
182 by ~17 deg. to the right. At the end of this phase, a second 2-min break was given and
183 prisms were replaced with control goggles by the experimenter. During the break,

184 participants kept their eyes closed and stayed motionless.
185 – POST-exposure phase: Participants first executed 30 reaching movements with the non-
186 exposed non-dominant arm (NDA), and then 30 movements with the dominant arm (DA)
187 (10 trials per target for each hand). For both blocks, the first presented target was the
188 central target (then target order was pseudo-randomised). For the NDA block, the second
189 target presented was the right target and the third target was the left target. For the DA
190 block, the second target presented was the left target and the third target was the right
191 target.

192 Participants were instructed not to move their opposite arm during or between trials.
193 An infra-red camera allowed continuous monitoring of participant's behaviour. The head was
194 unrestrained because stabilizing the head has been shown to preclude interlimb transfer of
195 prism adaptation (Hamilton 1964). The Prism exposure phase lasted approximately 20 min,
196 the complete reaching task lasting approximately 45 min.

197 Because previous work suggested that interlimb transfer depends on the perceived
198 source of motor errors (the credit-assignment issue; Berniker and Kording 2008), we aimed at
199 directly assessing the assignment of motor errors and determine whether it could influence
200 interlimb transfer. Immediately after the end of the reaching session, participants were asked
201 open questions to determine whether they consciously perceived errors in movement
202 trajectory during the first trials of the exposure phase. Then we showed a top view of each
203 participant's arm trajectory in the first trial of the exposure phase and asked participants to fill
204 a questionnaire. Participants were thus asked, in a counterbalanced order, 'Did you associate
205 the errors you made early in the exposure phase to external factors?' and 'Did you associate
206 the errors you made in the exposure phase to yourself (e.g., internal factors such as fatigue,
207 inattention...)?'. Participants answered these two questions by placing a mark on a 10-cm
208 scale. The left extremity (0) of the scale indicated 'Do not agree at all' and the other extremity

209 (10) indicated ‘Strongly agree’. Finally, participants had to estimate whether errors were
210 mostly associated with ‘Internal factors’ or ‘External factors’ by placing a mark on the scale
211 with ‘Internal factors’ on the left extremity of the scale and ‘External factors’ on the other
212 extremity.

213
214 *Kinematic data analysis*

215 Data, which are available upon request, were analysed using Matlab (Mathworks, Natick,
216 MA, USA). A few trials (0.9%) had to be discarded because they were not properly
217 performed by the participants or were corrupted by noise. Position data from the markers on
218 the right and left index fingertips were low-pass filtered with a dual-pass, no-lag Butterworth
219 (cut-off frequency: 8 Hz; order: 2). Movement onset was defined as the first-time hand
220 velocity reached 3 cm/s and movement offset as the first-time hand velocity dropped below 3
221 cm/s. Given that prisms mostly influence the direction of arm reaching movements, final
222 movement accuracy was computed as the angle between the vector from the start position to
223 the target position and the vector from the start position to the hand position at movement
224 offset. Initial movement direction was computed as the angle between the vector from the
225 start position to the target position and the vector from the start position to the hand position
226 at peak velocity (Wang & Sainburg 2003). Since peak velocity occurred around 150 ms after
227 movement onset in the present study, initial direction was considered the most critical
228 dependant variable because it mostly reflects the initial motor plan, before online visual
229 feedback can substantially influence movement direction (Reichenbach et al. 2014; Sarlegna
230 & Mutha 2015).

231
232 *Statistical analysis*

233 Using Statistica 8 (StatSoft, Tulsa, OK, USA), repeated-measures analyses of variances
234 (ANOVA) and t-tests allowed us to assess the significance of the results. First, to assess

235 adaptation of the DA, the mean data of the 10 movements toward the central target of the
236 PRE-exposure phase (baseline) were compared with i) the first trials and the last trial of the
237 Prism exposure phase (to analyse the effect of the visual perturbation induced by prisms and
238 the adaptation) and ii) the first trial of the POST-exposure phase (to analyse the after-effect).
239 The number of trials to adapt was computed by comparing for each participant a 95%
240 confidence interval of initial direction during the baseline PRE-exposure phase to the initial
241 direction of the first movements made during the Exposure phase. We determined the number
242 of trials which were necessary for initial direction during the Exposure phase to fall back
243 within the baseline's confidence interval. The after-effect value found on the DA of each
244 participant was defined as the initial direction of the 1st trial made during the POST-exposure
245 DA phase minus the mean of the initial direction of 10 trials made toward the central target
246 during the PRE-exposure DA phase. We also assessed whether adaptation of DA movements
247 toward the central target generalized across movement directions by comparing the mean data
248 of the PRE-exposure movements toward one of the lateral targets to the value of the first trial
249 in POST-exposure for the corresponding target.

250 To assess interlimb transfer of DA adaptation to the NDA, we compared the 10 NDA
251 movements toward the central target (0 deg.) of the PRE-exposure phase to the first NDA
252 movement of the POST-exposure phase (toward the central target). The transfer value of each
253 participant was defined as the initial direction of the 1st trial made during the POST-exposure
254 NDA phase minus the mean of the initial direction of 10 trials made toward the central target
255 (0 deg.) during the PRE-exposure NDA phase. All data had a normal distribution as verified
256 with the Kolmogorov-Smirnov method. Newman-Keuls tests were used for post-hoc analysis.
257 For all tests, the significance threshold was set at 0.05.

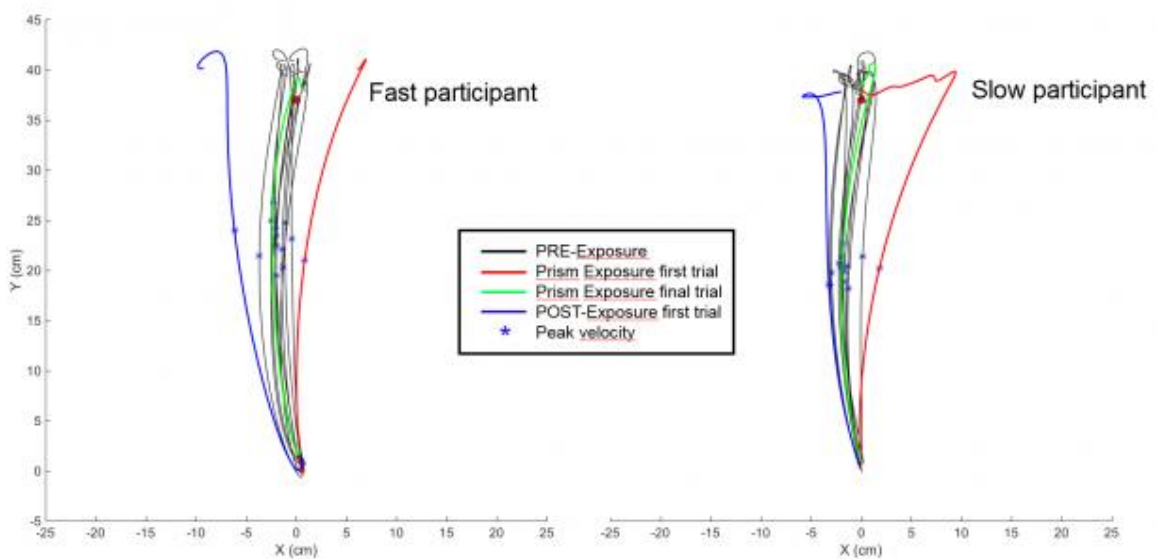
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259

260 **Results**

261 *Prismatic adaptation of dominant arm movements*

262 During the PRE-exposure experimental phase used to determine baseline performance,
263 reaching movements were generally accurate (mean \pm SD final error= 0.3 ± 0.5 deg.) despite
264 their high velocity (mean peak velocity across targets= 3.2 ± 0.7 m/s). Most kinematic
265 parameters did not substantially vary across the three phases of the session (PRE-exposure,
266 Prism exposure and POST-exposure) as ANOVAs showed no significant difference across
267 experimental phases (mean peak velocity across targets, arms and conditions= 3.1 ± 0.8 m/s,
268 $F(2,38)=0.1$, $p=0.87$, $\eta^2=0.007$; time to peak velocity= 154 ± 31 ms, $F(2,38)=0.13$, $p=0.88$,
269 $\eta^2=0.005$; peak acceleration = 43.8 ± 16.4 m/s², $F(2,38)=1.8$, $p=0.19$, $\eta^2=0.08$; time to peak
270 acceleration= 86 ± 32 ms, $F(2,38)=1.1$, $p=0.33$, $\eta^2=0.04$; movement time= 435 ± 103 ms;
271 $F(2,38)=2.7$, $p=0.08$, $\eta^2=0.12$).



272

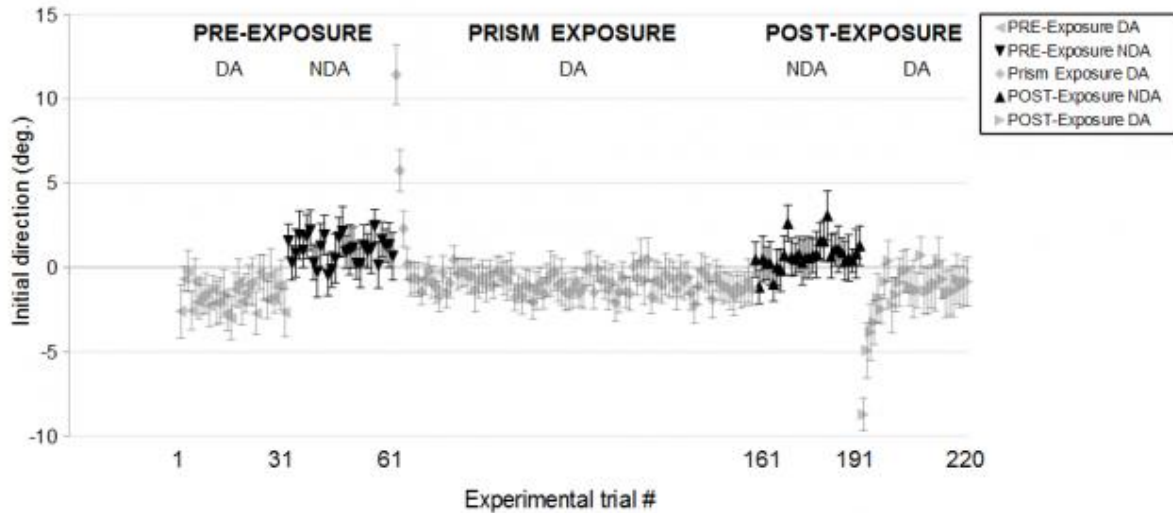
273 *Figure 2: Prism adaptation, illustrated with a top view of reaching movements with the*
274 *dominant arm for a fast participant (mean peak velocity across the experiment= 3.9 m/s) and*
275 *a slow participant (mean peak velocity across the experiment= 2.1 m/s). (Color required for*
276 *printed version).*

277

278 When participants had to wear prisms, which deviated the visual field to the right (thus
279 including the seen target which differed from its physical location), movement trajectory of

280 the first trial was deviated to the right. Compared to the fast participants, slower participants
281 had more time to visually compare hand and target positions and to correct for movement
282 errors. This can be seen in Figure 2 which illustrates the motor behavior of two participants
283 with different movement speeds. While all participants saw their hand going rightward with
284 respect to the target, slower participants could adjust the arm trajectory during the course of
285 the movement.

286 Adaptation was revealed by the reduction, trial after trial, of final errors as well as
287 trajectory errors, which eventually became similar to baseline (Figure 3, grey dots). Only the
288 central target was used during the Prism exposure phase and when only considering
289 movements toward the central target throughout the experiment, a one-way ANOVA [PHASE
290 (PRE-exposure, Prism exposure 1st trial, 2nd trial, 3rd trial, 4th trial and 100th trial, POST-
291 exposure 1st trial)] showed a significant effect of the experimental PHASE on initial
292 movement direction ($F(6,114)=55.9$, $p=0.0000$, $\eta^2=0.75$). Post-hoc comparisons revealed
293 that, as shown in Figure 4A, initial direction was significantly deviated to the right for the first
294 trial of the Prism exposure phase compared to baseline, i.e. to the mean of the 10 movements
295 toward the central target in the PRE-exposure phase; the shift was +12.8 deg. on average
296 across participants. Initial direction of the second and third movements of the Prism exposure
297 phase also differed from baseline, but the initial direction of the fourth trial did not
298 significantly differ from baseline, suggesting that it took about four trials for participants to
299 adapt to the prism perturbation; the average number of trials for movements to fall back
300 within the 95% confidence interval of the baseline was 4.7 ± 2.6 trials.



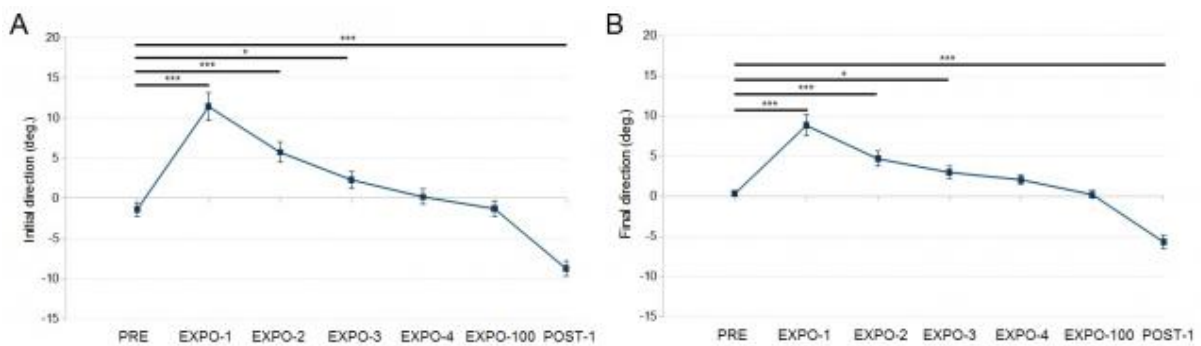
301

302 *Figure 3: Prism adaptation, illustrated with initial direction averaged across participants as*
 303 *a function of the experimental conditions. Error bars represent standard errors.*

304

305 Prisms also influenced final reach accuracy (Figure 4B). This was statistically
 306 significant as an ANOVA [PHASE (PRE-exposure, Prism exposure 1st trial, 2nd trial, 3rd trial,
 307 4th trial and 100th trial, POST-exposure 1st trial)] showed an effect of the experimental
 308 PHASE on final direction ($F(6,114)=42.1$, $p=0.0000$, $\eta^2=0.69$). Final direction was deviated
 309 rightward on the first trial of the Prism exposure phase compared to baseline (the shift was
 310 +8.5 deg. on average across participants). This analysis also suggests that adaptation occurred
 311 in about 4 trials.

312



313

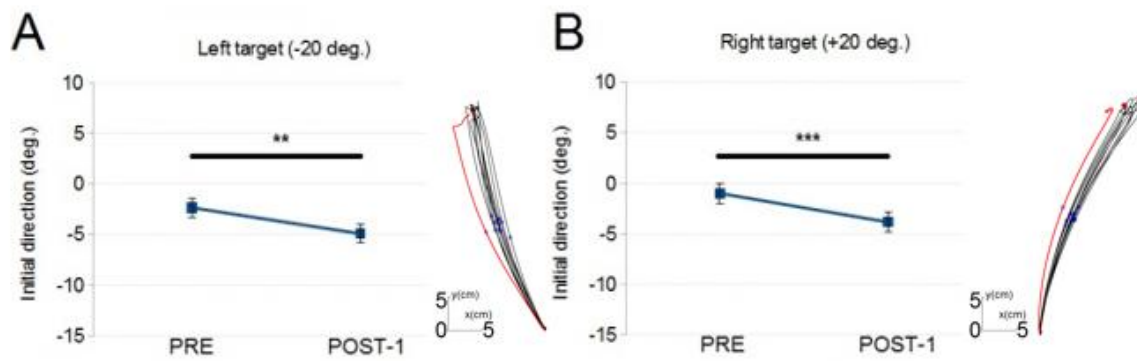
314 *Figure 4: Prism adaptation, illustrated with initial direction (A) and final direction (B) across*
 315 *experimental trials with the dominant arm. Data points represent the mean of 10 trials toward*
 316 *the central target during PRE-exposure, the 1st, 2nd, 3rd, 4th and 100th trial of the Prism*

317 *exposure phase, and the 1st trial of the POST-Exposure phase. Error bars represent standard*
318 *errors. * $p < 0.05$ *** $p < 0.001$, significant difference. (Color not required for printed version).*

319

320 After the Prism exposure phase, the rightward-deviating prisms were removed. Figures
321 2, 3 and 4 show that following the POST-exposure phase testing the non-dominant arm,
322 leftward after-effects were still observed on the dominant arm. Indeed, the first trial during the
323 POST-exposure phase with the dominant arm was deviated to the left compared to the PRE-
324 exposure phase (mean leftward shift in initial direction=7.3 deg.; mean shift in final
325 direction=6.0 deg.). The after-effect was systematic: when assessed for each participant by
326 comparing initial direction in the first trial of POST-exposure to the 95% confidence interval
327 of the baseline trials, the after-effect was significant for every single participant, further
328 reflecting prism adaptation.

329 While reaching movements were made only toward the central target during the Prism
330 exposure phase, different target directions were tested during the PRE- and the POST-
331 exposure phase to determine whether prism adaptation generalized across movement
332 directions. Figure 5 shows that after-effects were also found for the lateral targets. A t-test
333 showed a significant difference between initial direction of the first DA movement toward the
334 left target during the POST-exposure phase and the mean of the 10 trials made toward the left
335 target during the DA PRE-exposure phase ($t(20)=3.07$; $p=0.006$; Cohen's $d=0.04$; see Figure
336 5A). An equivalent difference was seen for DA reaches to the right target ($t(20)=4.18$;
337 $p=0.0005$; Cohen's $d=0.04$; see Figure 5B). These findings indicate generalization of prism
338 adaptation across target directions. Such generalization was also statistically significant when
339 analyzing final direction (for the left target: $t(20)=7.04$; $p=0.0000$; Cohen's $d=0.15$; and for
340 the right target: $t(20)=3.74$; $p=0.001$; Cohen's $d=0.1$).



341

342 *Figure 5: Generalization of prism adaptation across movement directions, illustrated with*
 343 *initial direction of the dominant arm (DA) toward the left target (A) and right target (B) for*
 344 *the PRE-exposure phase (mean of 10 trials) and the 1st trials of the POST-exposure phase*
 345 *toward the corresponding target. Error bars represent standard errors. ** $p < 0.01$*
 346 **** $p < 0.001$, significant difference. Insets present top views of dominant arm movements*
 347 *during the PRE-exposure phase (black lines) and the first trial of the POST-exposure phase*
 348 *(red line). (Color required for printed version).*

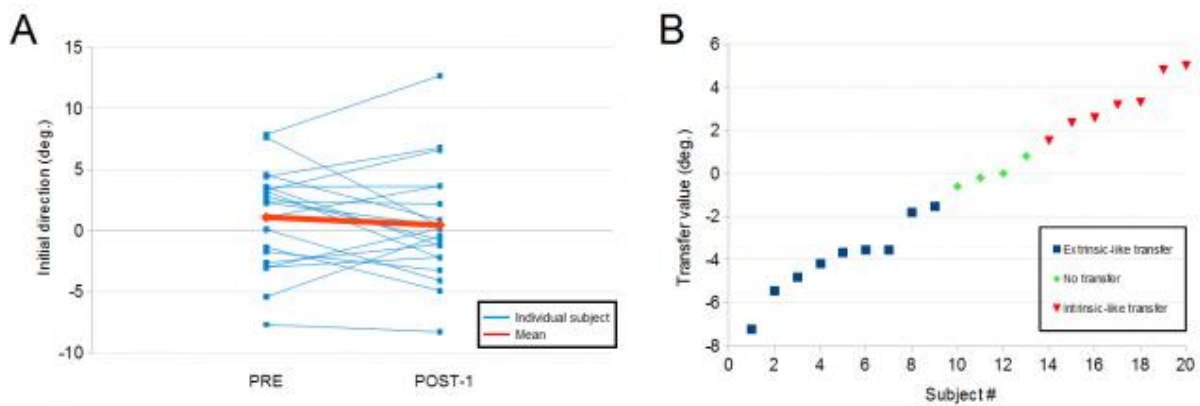
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350

351 *Heterogeneity of interlimb transfer of prism adaptation*

352 While prism adaptation and its generalization across directions were significant for the
 353 dominant arm across the group of 20 participants, there was no evidence of interlimb transfer
 354 at the group level (Figure 3, black dots, and 6). A t-test showed no significant difference
 355 between initial direction of the first movement (toward the central target) during NDA POST-
 356 exposure phase and the mean initial direction of the 10 trials made toward the same target
 357 during the NDA PRE-exposure phase ($t(20)=0.8$; $p=0.43$). In line with this finding, t-tests
 358 revealed no significant differences in initial direction when comparing the first NDA
 359 movement of the POST-exposure toward one of the lateral targets to the corresponding PRE-
 360 exposure (Left target: $t(19)=0.5$; $p=0.63$; Right target: $t(20)=1.0$; $p=0.32$). The analysis of
 361 final direction resulted in similar findings, i.e., the first NDA movement toward each target
 362 did not differ from its respective baseline (Central target: $t(20)=0.43$, $p=0.68$; Left target:
 363 $t(19)=0.45$, $p=0.66$; Right target: $t(20)=0.28$, $p=0.79$).

364

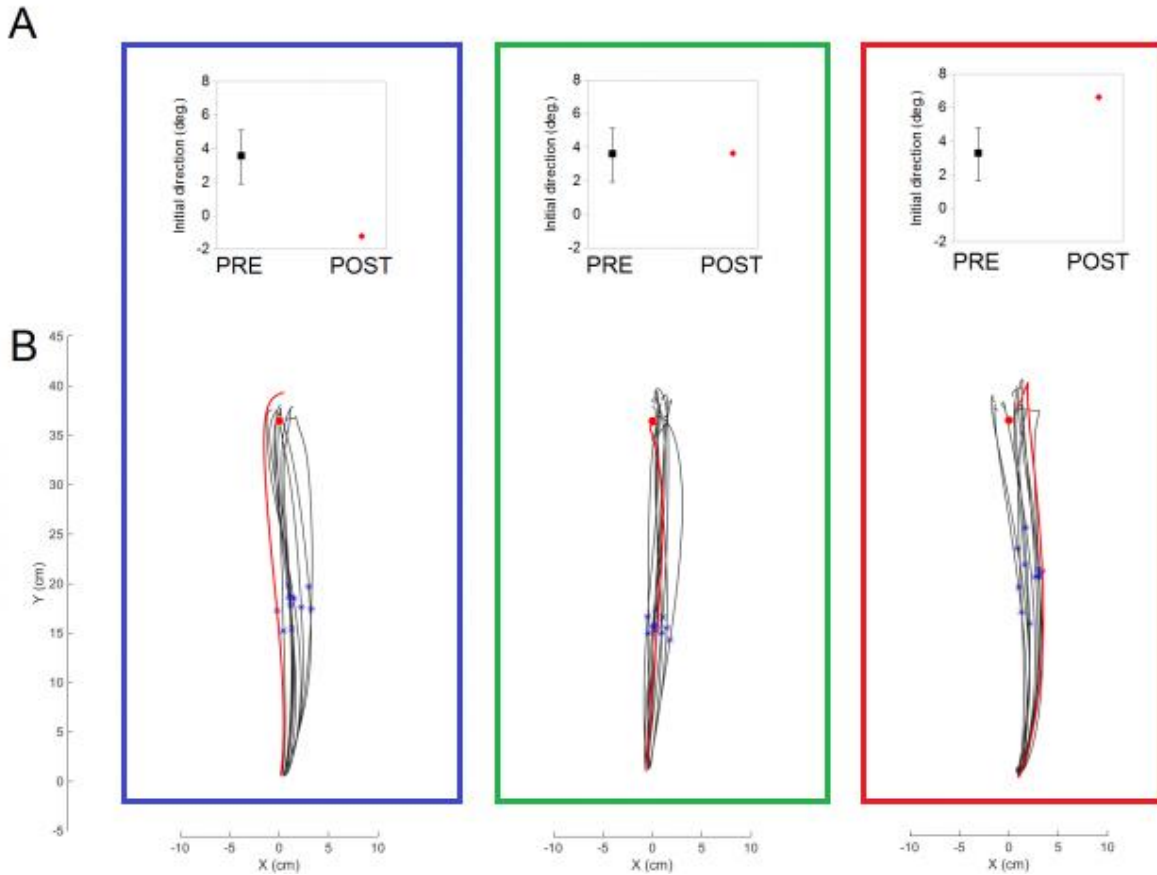


365

366 *Figure 6: A/ Initial direction of each participant with the non-dominant arm (blue lines)*
367 *across the PRE-exposure phase (mean of 10 trials) and for the 1st trial of the POST-exposure*
368 *phase. The mean initial direction across all participants is in red line. B/ Transfer value*
369 *(POST-1 – PRE) of each participant. (Color not required for printed version).*

370

371 Interlimb transfer was not significant because of large inter-individual differences, as shown
372 in Figures 6A and 6B. To determine whether interlimb transfer was present or not for each
373 participant, we computed a 95% confidence interval from all movements made by each
374 individual during the PRE-exposure of the NDA toward the central target. When the initial
375 direction of the first trial of POST-exposure NDA phase was within the confidence interval,
376 transfer was not considered to be significant. When the initial direction of the first trial of
377 POST-exposure NDA phase was below the lower limit of this confidence interval, transfer
378 was considered as leftward (opposite to the rightward prism shift) and referred to as
379 ‘extrinsic-like’ (Figure 7). In contrast, if it was greater than the upper limit of the confidence
380 interval, transfer was rightward and referred to as ‘intrinsic-like’. This analysis revealed that 9
381 participants exhibited transfer in the leftward (extrinsic-like) direction, 7 participants
382 exhibited rightward (intrinsic-like) transfer and 4 participants exhibited no transfer: such
383 heterogeneity clearly appears on Figure 6B and Figure 7, which highlights the continuum of
384 interlimb transfer across participants.



385

386 *Figure 7: Examples of interlimb transfer for three participants. A/ 95% Confidence intervals*
 387 *built from PRE-exposure data (black), contrasted with the first trial of the POST-exposure*
 388 *phase (red). B/ Top views of reaching movements with the non-dominant arm during the PRE-*
 389 *exposure phase (black lines) and the first trial of the POST-exposure phase (red line). In the*
 390 *left column, the first POST-exposure trial falls outside the confidence interval and the*
 391 *interlimb transfer is consistent with an ‘extrinsic-like’ movement representation. In the*
 392 *central column, there is no transfer and in the right column, transfer is ‘intrinsic-like’.*
 393 *(Color required for printed version).*

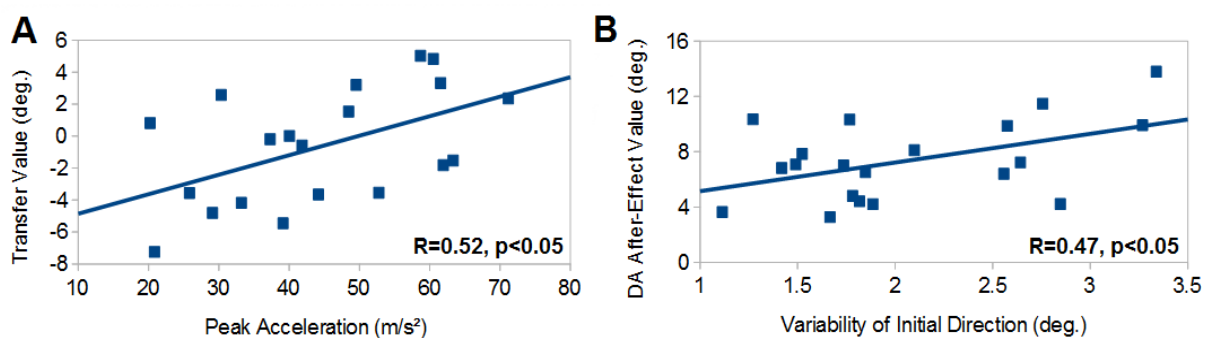
394

395 *Individual kinematic features correlate with the interlimb transfer value and after-effects of*
 396 *sensorimotor adaptation*

397 We aimed to determine whether individual characteristics of participants could be linked to
 398 the magnitude of transfer from the dominant to the non-dominant arm. We first assessed the
 399 influence of handedness on sensorimotor adaptation, but no significant correlation was found
 400 between handedness and transfer value ($r=-0.22$; $p=0.35$); handedness did not significantly
 401 influence or correlate with any measure related to sensorimotor adaptation or transfer.
 402 However, it has been suggested that movement variability and velocity could influence

403 sensorimotor adaptation (Kitazawa et al. 1997; Wu et al. 2014; Pekny et al. 2015; Lefumat et
 404 al. 2015; Therrien et al. 2016) and also distinguished the early and late phases of adaptation in
 405 terms of underlying mechanisms (Smith et al. 2006; Wolpert et al. 2011). We thus
 406 investigated the influence of peak velocity, peak acceleration and variable trajectory errors
 407 throughout adaptation or specifically during the early and late phases of Prism exposure (first
 408 and last 10 exposure trials). We found that interlimb transfer was correlated with variables
 409 typically associated to movement vigor, such as peak acceleration and peak velocity (Mazzoni
 410 et al. 2007; Reppert et al. 2018). Figure 8A shows a positive linear correlation between the
 411 transfer value and the mean peak acceleration averaged across the Prism exposure phase (PA
 412 $= 0.1 \times \text{transfer value} - 6$; $r=0.52$; $p=0.02$). Low peak acceleration reflected a negative
 413 transfer value (Figure 8A) and therefore extrinsic transfer while high peak acceleration
 414 reflected a positive transfer value and therefore intrinsic transfer. As expected across the
 415 Prism exposure phase, peak acceleration was correlated with peak velocity ($r=0.96$;
 416 $p=0.0000$). Peak velocity was also positively correlated with the transfer value ($r=0.48$;
 417 $p=0.03$).

418

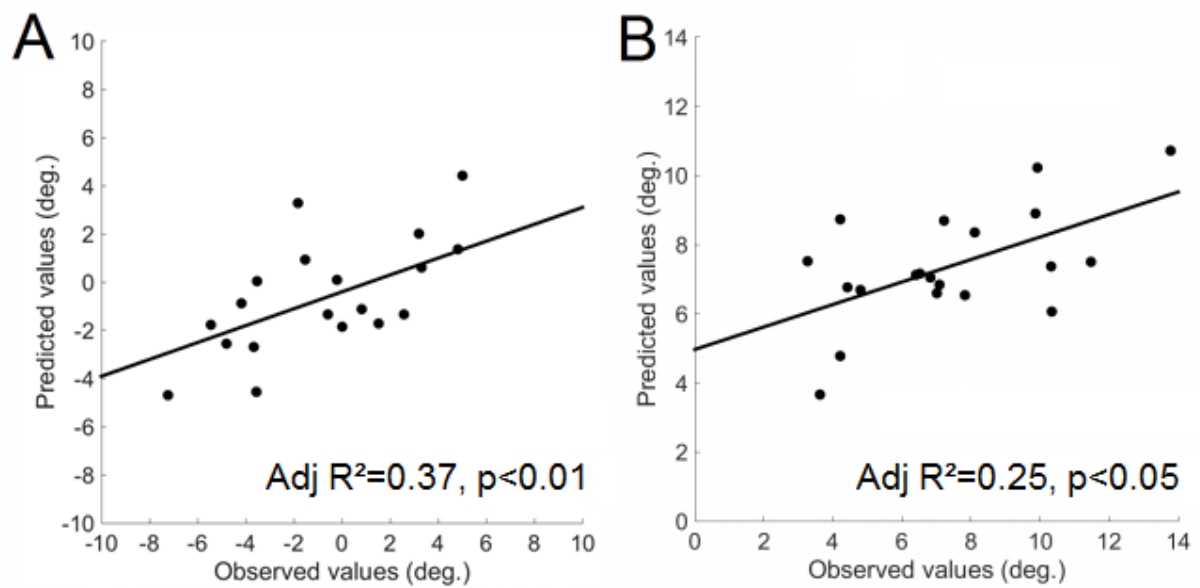


419

420 *Figure 8: A/ Correlation between interlimb transfer and mean peak acceleration averaged*
 421 *across the prism exposure phase. B/ Correlation between DA after-effect and variability of*
 422 *initial direction of the ten last trials of the prism exposure phase. (Color not required for*
 423 *printed version).*

424

425 To examine whether the magnitude of interlimb transfer could be correlated to a
426 combination of kinematic variables measured in early and late exposure phases, we used a
427 multiple regression analysis. A forward-stepwise method (accepting the most powerful
428 predictor first) revealed that variables such as, first, mean peak acceleration during the Prism
429 exposure phase and, second, variability of initial direction at the end of the Prism exposure
430 phase (last 10 trials) could be correlated with the observed transfer value [$F(2,17)=6.6$;
431 $r^2=0.44$; adjusted $r^2=0.37$; $p=0.007$]. The equation of the multiple regression was as follows:
432 transfer value = $-11.41 + 0.14 \times PA + 2.28 \times$ variability of initial direction, indicating that the
433 greater the peak acceleration, the greater the variability, the greater the transfer value. Low
434 peak acceleration and low variability reflected extrinsic transfer while high peak acceleration
435 and high variability reflected intrinsic transfer. The contributions of peak acceleration
436 ($p=0.006$) and variability ($p=0.036$) were both significant. Adding more kinematic variables
437 increased the percentage of explained variance (which reached 93% with 9 variables for
438 instance, including peak velocity and number of trials to adapt); we only report results with 2
439 variables for the sake of clarity. Figure 9A shows the relationship between the observed and
440 predicted transfer values based on the equation of the 2-variable multiple regression.



441

442 *Figure 9: A/ Observed versus predicted transfer based on a multiple regression with two*
 443 *measures, peak acceleration across the Prism exposure phase and variability of initial*
 444 *direction in the late exposure phase (last 10 trials). B/ Observed versus predicted DA after-*
 445 *effect (absolute value), based on a multiple regression using variability of initial direction in*
 446 *late exposure and number of exposure trials to adapt. (Color not required for printed*
 447 *version).*

448

449 We investigated a potential link between the transfer value and the after-effect value
 450 on the DA, but no significant correlation was found ($r=-0.37$; $p=0.1$). For the following
 451 analyses, we used the absolute value of the after-effect for clarity purposes (because all
 452 participants were deviated in the same direction during the DA POST-exposure 1st trial, so the
 453 greater the after-effect value, the more deviated to the left is the participant compared to
 454 his/her PRE-exposure phase). We found a positive linear correlation between variability of
 455 initial direction during the late exposure phase (last 10 trials) and the after-effect (Figure 8B;
 456 $r=0.47$; $p=0.04$). We also examined whether the magnitude of after-effect found on the DA
 457 could be correlated with kinematic data by using a multiple regression analysis, as we did for
 458 interlimb transfer. A forward-stepwise multiple regression revealed that late-exposure
 459 variability and the number of trials to adapt were the first two variables correlated with the
 460 observed after-effect value [$F(2,17)=4.1$; $r^2=0.32$; adjusted $r^2=0.25$; $p=0.03$]. The multiple

461 regression equation was: absolute after-effect value = $-5.03 + 1.91 \times \text{variability} - 0.35 \times$
462 number of trials, indicating that the greater the variability and the fewer trials needed to adapt,
463 the greater the after-effect. Figure 9B shows the relationship between the observed and the
464 predicted after-effect values based on the equation of the multiple regression.

465

466 *Interlimb transfer is not significantly influenced by the awareness of motor errors*

467 Only one participant answered that he was not consciously aware of the errors made during
468 the beginning of the exposure phase, although his initial direction was shifted by 6.5 deg.
469 compared to his baseline. When asked whether they associated their errors to external factors,
470 participants tended to agree (mean score= 8.0 ± 2.3 with 10 indicating 'strongly agree'). When
471 asked whether they associated the errors they made in the exposure phase to themselves,
472 participants tended to disagree (mean score= 2.7 ± 3.0). When participants had to report
473 whether they assigned trajectory errors to 'internal factors' (0) or 'external factors' (10), they
474 tended to assign their errors to external factors (mean score= 7.8 ± 2.2). No significant
475 correlation was found between the transfer value and the assignment of errors (all $r < 0.08$; all
476 $p > 0.51$).

477 With respect to the question 'internal factors' or 'external factors', only 3 of the
478 participants pointed toward 'internal factors' (mean score= 4.1 ± 0.8). When these 3
479 participants were asked 'Did you associate the errors you made in the exposure phase to
480 yourself?', all of them agreed (mean score= 7.0 ± 1.4). These 3 participants did not agree
481 when asked 'Did you associate the errors you made early in the Exposure phase to external
482 factors?' (mean score= 3.4 ± 0.3). The 17 other participants assigned their trajectory errors to
483 external factors (mean score= 8.4 ± 1.6). A Mann-Whitney non-parametric test showed that
484 the transfer value did not significantly depend on the assignment of errors (mean of 3

485 participants reporting ‘internal factors’ $= -1.0 \pm 5.1$ deg.; mean of 17 participants reporting
486 ‘external factors’ $= -0.6 \pm 3.5$ deg.; $p=0.71$).

487

488

489 **Discussion**

490 We aimed to test the hypothesis that specific features of movements can influence the
491 interlimb transfer of sensorimotor adaptation. We used a well-known visuomotor perturbation
492 (prismatic glasses) to induce sensorimotor adaptation and assessed generalization across
493 directions and interlimb transfer (Harris 1963; Martin et al. 1996; Kitazawa et al. 1997;
494 Morton & Bastian 2004; Michel et al. 2007). Prisms have been used to study the process of
495 visuomotor adaptation since the pioneering work of von Helmholtz (1867) and Stratton
496 (1896) and the acquired knowledge has been valuable, for instance for the rehabilitation of
497 strabismus or spatial neglect (Rossetti et al. 1998). For the practical purpose of personalized
498 training (Seidler et al. 2015) as well as for a better understanding of the factors which
499 influence transfer of sensorimotor adaptation, we re-investigated the interlimb transfer of
500 prism adaptation with detailed analyses of movement kinematics for each individual.

501

502 *Generalization of prismatic adaptation across movement directions*

503 A classical pattern of prism adaptation was observed with the dominant arm: as in previous
504 studies (Redding & Wallace 1988; Martin et al. 1996; Sarlegna et al. 2007; O’Shea et al.
505 2014), initial errors due to the prisms were reduced trial-by-trial and when prisms were
506 removed, clear after-effects were observed with the trained limb. Such after-effects were
507 observed after participants reached to the same central target as in the Prism exposure phase.
508 After-effects were also observed on the two other lateral targets, consistent with previous
509 reports of generalization of sensorimotor adaptation across movement directions for prism

510 adaptation (Redding & Wallace 2006), visuomotor rotations (Ghahramani et al. 1996;
511 Krakauer et al. 2000) and adaptation to force fields (Thoroughman & Shadmehr 2000; Malfait
512 et al. 2002; Lefumat et al. 2015).

513 A prismatic perturbation biases all visual inputs, including vision of the environment,
514 the target and the arm, and would seem to facilitate generalization across the workspace or
515 even across tasks or limbs. For instance, generalization of prism adaptation has been
516 previously reported across upper-limb segments in a proximodistal direction (Hay and
517 Brouchon 1972; see also Krakauer et al. 2006) and from a walking task to a reaching task
518 (Morton and Bastian 2004). Generalization seems to be often found between tasks involving
519 similar joints (Alexander et al. 2011) or when adaptation involves higher-order, cognitive
520 processes (Morton & Bastian 2004; Malfait & Ostry 2004; McDougle et al. 2016).

521

522 *Interlimb transfer of prismatic adaptation*

523 To determine whether sensorimotor adaptation is limb specific, a classic test is to determine
524 whether adaptation with one arm influences the opposite arm. As early as 1963, Harris
525 reported that interlimb transfer of prism adaptation was limited. In the present study,
526 interlimb transfer was not significant at the group level and a large heterogeneity across
527 participants was uncovered. This appears to be consistent with the heterogeneity of findings
528 in the literature. At an individual level, we found that for some of the participants (N=4),
529 there was no interlimb transfer of prism adaptation, in line with the overall finding in several
530 previous studies (Kitazawa et al. 1997; Martin et al. 1996; Michel et al. 2007). For other
531 participants (N=9), interlimb transfer was observed in the form of leftward after-effects on
532 the non-dominant arm, which could reflect the leftward compensation of the rightward
533 prism deviation, in extrinsic or visual space (Harris 1963; Cohen 1967; Cohen 1973; Taub &
534 Goldberg 1973; Choe & Welch 1974; Wallace & Redding 1979). However, a second,

535 intrinsic coordinate system can be considered (Criscimagna-Hemminger et al. 2003; Galea
536 et al. 2007; Wiestler et al. 2014; Franklin et al. 2016). Representation in this coordinate
537 system predicts mirror-symmetric interlimb transfer with respect to the sagittal plane. In our
538 study, rightward interlimb transfer was observed in one third of the group (N=7), which may
539 reflect the encoding of sensorimotor adaptation in intrinsic space. This finding was
540 unexpected but is consistent with the work of Kalil and Freedman (1966) which reported a
541 large heterogeneity in interlimb transfer of prism adaptation. In particular, they reported that
542 two out of nine participants exhibited transfer which was consistent with an encoding of
543 prism adaptation in intrinsic coordinates.

544 One can speculate that behavioral heterogeneity, such as observed in the present
545 study, is related to the heterogeneity of the brain structures (Gazzaniga et al. 1998; ten
546 Donkelaar et al. 2004; Sun et al. 2016) or of the idiosyncratic representations underlying
547 visuomotor and force-field adaptation, as they appear to be encoded in both extrinsic and
548 intrinsic coordinates (Brayanov et al. 2012; Carroll et al. 2014; Wiestler et al. 2014;
549 Berniker et al. 2014; Parmar et al. 2015). The presence in pre-motor and motor areas of both
550 extrinsic-like and intrinsic-like representations (Takei et al. 1999; Takei et al. 2001;
551 Wiestler et al. 2014) may explain why interlimb transfer can be so heterogeneous across
552 studies, even when similar perturbations are used. Indeed, conflicting findings have been
553 reported for prism adaptation but also for adaptation to new limb dynamics (Criscimagna-
554 Hemminger et al. 2003; Malfait & Ostry 2004; Galea et al. 2007; Stockinger et al. 2015;
555 Lefumat et al. 2015). Next, we address the issue of whether one can make sense of that
556 heterogeneity.

557

558 *On the correlation between kinematic variables, interlimb transfer and after-effects*

559 Heterogeneity between individuals is inevitable when considering the idiosyncratic properties
560 of the central nervous system for any given individual (Gazzaniga et al. 1998; Kanai & Rees
561 2011). In the present study, a continuum of transfer values was observed. Regression analyses
562 showed that kinematic variables selected during the Prism exposure phase can be correlated
563 with the transfer value of each participant. We found that peak acceleration and peak velocity
564 during prism exposure, as well as variability of initial direction at the end of the exposure
565 phase, were related to interlimb transfer. Mazzoni et al. (2007) as well as Reppert et al. (2018)
566 highlighted how variables related to movement vigor, peak velocity or peak acceleration, for
567 instance, vary across individuals, possibly because of differences in perceived motor cost.
568 Kitazawa et al. (1997) previously highlighted the importance of peak velocity in prism
569 adaptation when they showed that the magnitude of the after-effect depends on the velocity
570 difference between movements during and after the exposure phase (see also Mattar & Ostry
571 2010).

572 In the present study, a higher peak acceleration (and peak velocity) was found for
573 participants who transferred in an intrinsic coordinate system, while a lower peak acceleration
574 corresponded to an extrinsic coordinate system. The influence of movement kinematics on
575 interlimb transfer may be mediated by the attribution of motor errors to different sources,
576 which has been suggested to be key for the pattern of generalization of sensorimotor
577 adaptation (Berniker & Kording 2008). However, assessing error-attribution is difficult and
578 our questionnaire-based approach failed to reveal a significant link between the source of
579 motor errors and interlimb transfer.

580 A parsimonious interpretation of these findings is that the way the new sensorimotor
581 mapping was learned during exposure influenced subsequent movements, including those
582 used to assess interlimb transfer. This is consistent with the idea that generalization of
583 sensorimotor adaptation depends on the history of prior actions (Krakauer et al. 2006; Wei &

584 Kording 2009). An alternative hypothesis is that there is a possible link between the
585 speed/acceleration of a movement and the nature of its neural representation. This may be
586 related to the idea that faster movements mostly rely on feedforward control, because less
587 time is available to process peripheral sensory feedback during movement execution.
588 Feedforward motor control describes how motor neurons control muscles without using
589 sensory feedback, most likely with signals in an intrinsic, muscle-based coordinate system
590 (Tanaka & Sejnowski 2013). Slower movements can be controlled with online feedback to
591 adjust the hand path, and the importance of visual feedback in human movement control has
592 been highlighted (Reichenbach et al. 2014; Sarlegna & Mutha 2015). The fact that visual
593 feedback control relies on the use of signals originally in extrinsic, retina-based coordinates,
594 may be related to the encoding of slower visually-guided movements in extrinsic coordinates.
595 Hence our findings suggest that movement vigor could explain the heterogeneity of interlimb
596 transfer reported in previous prism adaptation studies, in which unfortunately movement
597 speed or acceleration was rarely reported.

598 Our findings showed that variability of initial direction during the Prism exposure
599 phase was positively correlated with interlimb transfer to the non-dominant arm and to after-
600 effects on the adapted limb. High motor variability reflected intrinsic transfer while low
601 variability reflected extrinsic transfer. Variability is often considered to reflect noise in the
602 nervous system (Faisal et al. 2008) but recent findings highlighted how it can also reflect
603 exploration strategies and may benefit sensorimotor adaptation (Wu et al. 2014; Herzfeld &
604 Shadmehr 2014; Lefumat et al. 2015; Therrien et al. 2016; Lefumat et al. 2016; but see He et
605 al. 2016). For instance, Lefumat et al. (2015) found that participants who were more variable
606 when adapting to novel limb dynamics showed greater interlimb transfer. Our results on a
607 different type of adaptation (Haith & Vijayakumar 2009; Sarlegna & Bernier 2010; Donchin
608 et al. 2012) support and extend the idea that variability of the motor output could influence

609 after-effects on the trained as well as the untrained arm. However, further work is necessary
610 to understand the underlying mechanisms.

611 Handedness has been shown to affect interlimb transfer (Chase & Seidler 2008;
612 Lefumat et al. 2015) so we recruited both right- and left-handers to provide a general model
613 of interlimb transfer of prism adaptation. Lefumat et al. (2015) studied a population of 20
614 strongly right-handed individuals and reported that laterality quotient influenced interlimb
615 transfer of force-field adaptation. In our study, handedness or laterality quotient did not
616 significantly influence interlimb transfer of prism adaptation. However, across right- and
617 left-handers, a small set of movement characteristics such as movement acceleration or
618 variability during exposure was correlated to interlimb transfer. Now that a few movement
619 characteristics have been identified as related to interlimb transfer, further studies need to be
620 conducted in order to explore a possible causal link between these features and interlimb
621 transfer, for instance by assessing the effect of manipulating movement speed or variability.
622 Alternatively, future work could determine whether a third factor is the key leading to the
623 differences in, and the correlation between, kinematic variables and interlimb transfer.
624 Finally, it should be noted that in the present study, after-effects were systematically found
625 on the dominant arm in the POST-exposure phase that followed thirty non-dominant arm
626 movements with true visual feedback. Thus, the de-adaptation of non-dominant arm
627 movements did not completely wash out adaptation of the dominant arm. This indicates that
628 if there is any interlimb transfer from the non-dominant to the dominant arm, it is not
629 complete.

630

631 In conclusion, interlimb transfer resulted for some participants in a directional shift of
632 non-dominant arm movements that was consistent with an encoding of visuomotor adaptation
633 in extrinsic coordinates while, for other participants, interlimb transfer was consistent with an

634 encoding of sensorimotor adaptation in intrinsic coordinates. A detailed kinematic analysis
635 was instrumental to find that individual movement features such as movement acceleration
636 and variability were related to qualitative as well as quantitative aspects of sensorimotor
637 adaptation and its transfer across limbs. Low peak acceleration and low variability displayed
638 during the exposure phase were linked to an extrinsic type of transfer while high peak
639 acceleration and high variability were linked to an intrinsic type of transfer. Overall, these
640 findings on unconstrained movements support the idea that individual movement features
641 could be linked to the way the nervous system learn new motor skills and generalize learning.
642 The study also suggests that the preferred movement characteristics may be related to the
643 preferred coordinate frames of action representations.

644

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649

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651

652 **Compliance with Ethical Standards / Ethical approval:** All procedures performed in this
653 study involving human participants were in accordance with the ethical standards of the
654 institutional review board of the Institute of Movement Sciences and with the 1964 Helsinki
655 declaration and its later amendments or comparable ethical standards.

656

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659 **Author contributions:** A.G.R., H.L., J.-L.V., L.B. and F.R.S. designed the experiment;
660 A.G.R., H.L. and F.R.S. performed experiments; A.G.R. and F.R.S. analyzed data; A.G.R.
661 prepared figures; A.G.R., H.L., J.-L.V., R.C.M., L.B., C.B. and F.R.S. interpreted results of
662 experiments; A.G.R. and F.R.S. drafted manuscript; A.G.R., H.L., J.-L.V., R.C.M., L.B., C.B.
663 and F.R.S. edited manuscript and approved the final version for submission.

664 **References**

- 665 Alexander, M. S., Flodin, B. W., & Marigold, D. S. (2011). Prism adaptation and
666 generalization during visually guided locomotor tasks. *Journal of Neurophysiology*, *106*(2),
667 860–871.
- 668 Berniker, M., Franklin, D. W., Flanagan, J. R., Wolpert, D. M., & Kording, K. (2013). Motor
669 learning of novel dynamics is not represented in a single global coordinate system:
670 evaluation of mixed coordinate representations and local learning. *Journal of*
671 *Neurophysiology*, *111*(6), 1165–1182.
- 672 Berniker, M., & Kording, K. (2008). Estimating the sources of motor errors for adaptation and
673 generalization. *Nature Neuroscience*, *11*(12), 1454.
- 674 Brayanov, J. B., Press, D. Z., & Smith, M. A. (2012). Motor memory is encoded as a gain-
675 field combination of intrinsic and extrinsic action representations. *Journal of Neuroscience*,
676 *32*(43), 14951–14965.
- 677 Carroll, T. J., Poh, E., & de Rugy, A. (2014). New visuomotor maps are immediately
678 available to the opposite limb. *Journal of Neurophysiology*, *111*(11), 2232–2243.
- 679 Chase, C., & Seidler, R. (2008). Degree of handedness affects intermanual transfer of skill
680 learning. *Experimental Brain Research*, *190*(3), 317–328.
- 681 Choe, C. S., & Welch, R. B. (1974). Variables affecting the intermanual transfer and decay of
682 prism adaptation. *Journal of Experimental Psychology*, *102*(6), 1076.
- 683 Cohen, M. M. (1967). Continuous versus terminal visual feedback in prism aftereffects.
684 *Perceptual and Motor Skills*, *24*(3), 1295–1302.
- 685 Cohen, M. M. (1973). Visual feedback, distribution of practice, and intermanual transfer of
686 prism aftereffects. *Perceptual and Motor Skills*, *37*(2), 599–609.

687 Criscimagna-Hemminger, S. E., Donchin, O., Gazzaniga, M. S., & Shadmehr, R. (2003).
688 Learned dynamics of reaching movements generalize from dominant to nondominant arm.
689 *Journal of Neurophysiology*, *89*(1), 168–176.

690 DiZio, P., & Lackner, J. R. (1995). Motor adaptation to Coriolis force perturbations of
691 reaching movements: endpoint but not trajectory adaptation transfers to the nonexposed arm.
692 *Journal of Neurophysiology*, *74*(4), 1787–1792.

693 Donchin, O., Rabe, K., Diedrichsen, J., Lally, N., Schoch, B., Gizewski, E. R., & Timmann,
694 D. (2011). Cerebellar regions involved in adaptation to force field and visuomotor
695 perturbation. *Journal of Neurophysiology*, *107*(1), 134–147.

696 Faisal, A. A., Selen, L. P., & Wolpert, D. M. (2008). Noise in the nervous system. *Nature*
697 *Reviews Neuroscience*, *9*(4), 292.

698 Franklin, D. W., Batchelor, A. V., & Wolpert, D. M. (2016). The sensorimotor system can
699 sculpt behaviorally relevant representations for motor learning. *eNeuro*, *3*(4), ENEURO–
700 0070.

701 Galea, J. M., Miall, R. C., & Woolley, D. G. (2007). Asymmetric interlimb transfer of
702 concurrent adaptation to opposing dynamic forces. *Experimental Brain Research*, *182*(2),
703 267–273.

704 Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (1998). *Cognitive Neuroscience: The Biology*
705 *of the Mind* WW Norton & Co. *New York*.

706 Ghahramani, Z., Wolpert, D. M., & Jordan, M. I. (1996). Generalization to local remappings
707 of the visuomotor coordinate transformation. *Journal of Neuroscience*, *16*(21), 7085–7096.

708 Haith, A., & Vijayakumar, S. (2009). Implications of different classes of sensorimotor
709 disturbance for cerebellar-based motor learning models. *Biological Cybernetics*, *100*(1), 81–
710 95.

711 Hamilton, C. R. (1964). Intermanual transfer of adaptation to prisms. *The American Journal*
712 *of Psychology*, 77(3), 457–462.

713 Harris, C. S. (1963). Adaptation to displaced vision: visual, motor, or proprioceptive change?
714 *Science*, 140(3568), 812–813.

715 Hay, L., & Brouchon, M. (1972). Analysis of reorganization of visuomotor coordination in
716 humans. Generalization of adaptation to prismatic deviation of the visual space. *L'annee*
717 *psychologique*, 72(1), 25–38.

718 Held, R., & Freedman, S. J. (1963). Plasticity in human sensorimotor control. *Science*,
719 142(3591), 455–462.

720 Herzfeld, D. J., & Shadmehr, R. (2014). Motor variability is not noise, but grist for the
721 learning mill. *Nature Neuroscience*, 17(2), 149.

722 Joiner, W. M., Brayanov, J. B., & Smith, M. A. (2013). The training schedule affects the
723 stability, not the magnitude, of the interlimb transfer of learned dynamics. *Journal of*
724 *Neurophysiology*, 110(4), 984–998.

725 Kakei, S., Hoffman, D. S., & Strick, P. L. (1999). Muscle and movement representations in
726 the primary motor cortex. *Science*, 285(5436), 2136–2139.

727 Kakei, S., Hoffman, D. S., & Strick, P. L. (2001). Direction of action is represented in the
728 ventral premotor cortex. *Nature Neuroscience*, 4(10), 1020.

729 Kalil, R. E., & Freedman, S. J. (1966). Intermanual transfer of compensation for displaced
730 vision. *Perceptual and Motor Skills*, 22(1), 123–126.

731 Kanai, R., & Rees, G. (2011). The structural basis of inter-individual differences in human
732 behaviour and cognition. *Nature Reviews Neuroscience*, 12(4), 231.

733 Kitazawa, S., Kimura, T., & Uka, T. (1997). Prism adaptation of reaching movements:
734 specificity for the velocity of reaching. *Journal of Neuroscience*, 17(4), 1481–1492.

735 Krakauer, J. W., Mazzoni, P., Ghazizadeh, A., Ravindran, R., & Shadmehr, R. (2006).
736 Generalization of motor learning depends on the history of prior action. *PLoS Biology*,
737 4(10), e316.

738 Krakauer, J. W., Pine, Z. M., Ghilardi, M.-F., & Ghez, C. (2000). Learning of visuomotor
739 transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience*,
740 20(23), 8916–8924.

741 Lefumat, H. Z., Miall, R. C., Cole, J. D., Bringoux, L., Bourdin, C., Vercher, J.-L., &
742 Sarlegna, F. R. (2016). Generalization of force-field adaptation in proprioceptively-
743 deafferented subjects. *Neuroscience Letters*, 616, 160–165.

744 Lefumat, H. Z., Vercher, J.-L., Miall, R. C., Cole, J., Buloup, F., Bringoux, L., Bourdin, C., &
745 Sarlegna, F. R. (2015). To transfer or not to transfer? Kinematics and laterality quotient
746 predict interlimb transfer of motor learning. *Journal of Neurophysiology*, 114(5), 2764–
747 2774.

748 Malfait, N., & Ostry, D. J. (2004). Is interlimb transfer of force-field adaptation a cognitive
749 response to the sudden introduction of load? *Journal of Neuroscience*, 24(37), 8084–8089.

750 Malfait, N., Shiller, D. M., & Ostry, D. J. (2002). Transfer of motor learning across arm
751 configurations. *Journal of Neuroscience*, 22(22), 9656–9660.

752 Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996).
753 Throwing while looking through prisms: II. Specificity and storage of multiple gaze—throw
754 calibrations. *Brain*, 119(4), 1199–1211.

755 Mattar, A. A., & Ostry, D. J. (2010). Generalization of dynamics learning across changes in
756 movement amplitude. *Journal of Neurophysiology*, 104(1), 426–438.

757 Mazzoni, P., Hristova, A., & Krakauer, J. W. (2007). Why don't we move faster? Parkinson's
758 disease, movement vigor, and implicit motivation. *Journal of Neuroscience*, 27(27), 7105-
759 7116.

760 McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking aim at the cognitive side of
761 learning in sensorimotor adaptation tasks. *Trends in Cognitive Sciences*, *20*(7), 535–544.

762 Michel, C., Pisella, L., Prablanc, C., Rode, G., & Rossetti, Y. (2007). Enhancing visuomotor
763 adaptation by reducing error signals: single-step (aware) versus multiple-step (unaware)
764 exposure to wedge prisms. *Journal of Cognitive Neuroscience*, *19*(2), 341–350.

765 Morton, S. M., & Bastian, A. J. (2004). Prism adaptation during walking generalizes to
766 reaching and requires the cerebellum. *Journal of Neurophysiology*, *92*(4), 2497–2509.

767 Mostafa, A. A., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. (2014). Intermanual
768 transfer and proprioceptive recalibration following training with translated visual feedback
769 of the hand. *Experimental Brain Research*, *232*(6), 1639–1651.

770 Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory.
771 *Neuropsychologia*, *9*(1), 97–113.

772 O’Shea, J., Gaveau, V., Kandel, M., Koga, K., Susami, K., Prablanc, C., & Rossetti, Y.
773 (2014). Kinematic markers dissociate error correction from sensorimotor realignment during
774 prism adaptation. *Neuropsychologia*, *55*, 15–24.

775 Parmar, P. N., Huang, F. C., & Patton, J. L. (2015). Evidence of multiple coordinate
776 representations during generalization of motor learning. *Experimental Brain Research*,
777 *233*(1), 1–13.

778 Pekny, S. E., Izawa, J., & Shadmehr, R. (2015). Reward-dependent modulation of movement
779 variability. *Journal of Neuroscience*, *35*(9), 4015–4024.

780 Redding, G. M., & Wallace, B. (1988). Components of prism adaptation in terminal and
781 concurrent exposure: Organization of the eye-hand coordination loop. *Perception &*
782 *Psychophysics*, *44*(1), 59–68.

783 Redding, G. M., & Wallace, B. (2006). Generalization of prism adaptation. *Journal of*
784 *Experimental Psychology: Human Perception and Performance*, *32*(4), 1006.

785 Reichenbach, A., Franklin, D. W., Zatska-Haas, P., & Diedrichsen, J. (2014). A dedicated
786 binding mechanism for the visual control of movement. *Current Biology*, *24*(7), 780–785.

787 Reppert, T. R., Rigas, I., Herzfeld, D. J., Sedaghat-Nejad, E., Komogortsev, O., & Shadmehr,
788 R. (2018). Movement vigor as a traitlike attribute of individuality. *Journal of*
789 *Neurophysiology*, *120*(2), 741-757.

790 Rossetti, Y., Rode, G., Pisella, L., Farné, A., Li, L., Boisson, D., & Perenin, M.-T. (1998).
791 Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect.
792 *Nature*, *395*(6698), 166.

793 Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. *Frontiers*
794 *in Psychology*, *5*, 1092.

795 Sarlegna, F. R., & Bernier, P. M. (2010). On the link between sensorimotor adaptation and
796 sensory recalibration. *Journal of Neuroscience*, *30*(35), 11555–11557.

797 Sarlegna, F. R., Gauthier, G. M., & Blouin, J. (2007). Influence of feedback modality on
798 sensorimotor adaptation: Contribution of visual, kinesthetic, and verbal cues. *Journal of*
799 *Motor Behavior*, *39*(4), 247–258.

800 Sarlegna, F. R., & Mutha, P. K. (2015). The influence of visual target information on the
801 online control of movements. *Vision Research*, *110*, 144–154.

802 Seidler, R. D., Mulavara, A. P., Bloomberg, J. J., & Peters, B. T. (2015). Individual predictors
803 of sensorimotor adaptability. *Frontiers in Systems Neuroscience*, *9*, 100.

804 Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with
805 different timescales underlie short-term motor learning. *PLoS Biology*, *4*(6), e179.

806 Stockinger, C., Thüerer, B., Focke, A., & Stein, T. (2015). Intermanual transfer characteristics
807 of dynamic learning: direction, coordinate frame, and consolidation of interlimb
808 generalization. *Journal of Neurophysiology*, *114*(6), 3166–3176.

809 Stratton, G. M. (1896). Some preliminary experiments on vision without inversion of the
810 retinal image. *Psychological Review*, 3(6), 611.

811 Sun, Z. Y., Pinel, P., Rivière, D., Moreno, A., Dehaene, S., & Mangin, J.-F. (2016). Linking
812 morphological and functional variability in hand movement and silent reading. *Brain*
813 *Structure and Function*, 221(7), 3361–3371.

814 Tanaka, H., & Sejnowski, T. J. (2013). Computing reaching dynamics in motor cortex with
815 Cartesian spatial coordinates. *Journal of Neurophysiology*, 109(4), 1182–1201.

816 Taub, E., & Goldberg, I. A. (1973). Prism adaptation: control of intermanual transfer by
817 distribution of practice. *Science*, 180(4087), 755–757.

818 Taylor, J. A., Wojaczynski, G. J., & Ivry, R. B. (2011). Trial-by-trial analysis of intermanual
819 transfer during visuomotor adaptation. *Journal of Neurophysiology*, 106(6), 3157–3172.

820 Ten Donkelaar, H. J., Lammens, M., Wesseling, P., Hori, A., Keyser, A., & Rotteveel, J.
821 (2004). Development and malformations of the human pyramidal tract. *Journal of*
822 *Neurology*, 251(12), 1429–1442.

823 Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2015). Effective reinforcement learning
824 following cerebellar damage requires a balance between exploration and motor noise. *Brain*,
825 139(1), 101–114.

826 Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive
827 combination of motor primitives. *Nature*, 407(6805), 742.

828 Vangheluwe, S., Suy, E., Wenderoth, N., & Swinnen, S. P. (2006). Learning and transfer of
829 bimanual multifrequency patterns: effector-independent and effector-specific levels of
830 movement representation. *Experimental Brain Research*, 170(4), 543–554.

831 Von Helmholtz, H. (1867). *Handbuch der physiologischen Optik* (Vol. 9). Voss.

832 Wallace, B., & Redding, G. M. (1979). Additivity in prism adaptation as manifested in
833 intermanual and interocular transfer. *Perception & Psychophysics*, 25(2), 133–136.

- 834 Wang, J., & Sainburg, R. L. (2003). Mechanisms underlying interlimb transfer of visuomotor
835 rotations. *Experimental Brain Research*, *149*(4), 520–526.
- 836 Wei, K., & Kording, K. (2009). Relevance of error: what drives motor adaptation? *Journal of*
837 *Neurophysiology*, *101*(2), 655–664.
- 838 Wiestler, T., Waters-Metenier, S., & Diedrichsen, J. (2014). Effector-independent motor
839 sequence representations exist in extrinsic and intrinsic reference frames. *Journal of*
840 *Neuroscience*, *34*(14), 5054–5064.
- 841 Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor
842 learning. *Nature Reviews Neuroscience*, *12*(12), 739.
- 843 Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P., & Smith, M. A. (2014).
844 Temporal structure of motor variability is dynamically regulated and predicts motor learning
845 ability. *Nature Neuroscience*, *17*(2), 312.